

On Sinistral Coiling among Fossil North American Lymnaeidae

by

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Abstract. A study of sinistral coiling among fossil members of the genus *Lymnaea* in North America shows that such coiling exists, but is uncommon. *Lymnaea ambiguspira* nom. nov. and *L. tulameenensis*, with its sinistral morph "*Aplexa ricei*," are ambidextrous species in which both sinistrally and dextrally coiled individuals are known to exist. *Lymnaea saxarubrensis*, *L. disjuncta*, and *L. bridgerensis* are apparently consistent sinistral species. These species range from Paleocene (or latest Cretaceous?) to early Miocene in age. A new name, *Lymnaea ambiguspira*, is proposed for the preoccupied *Lymnaea vetusta ambigua* Pierce, 1993.

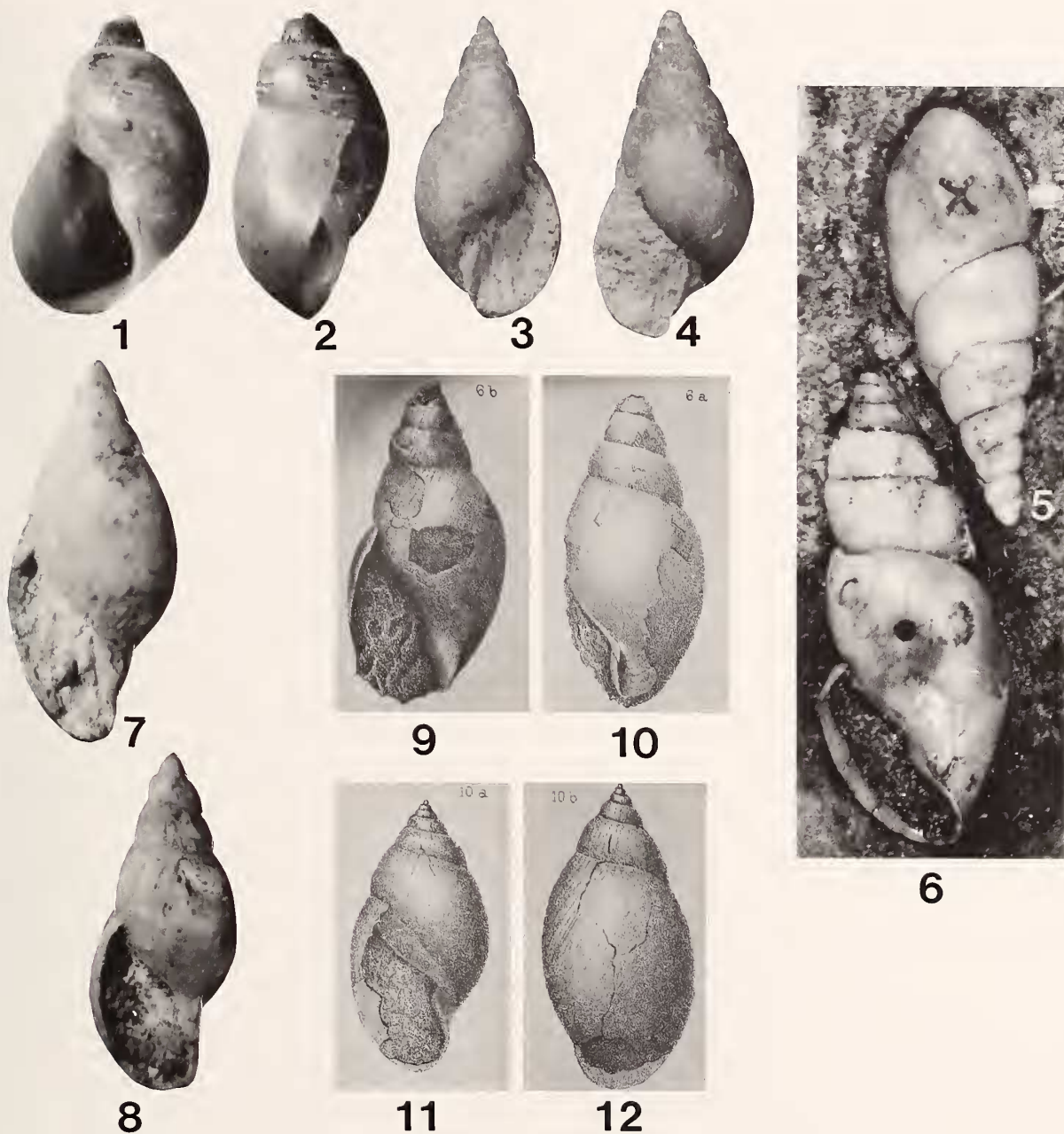
INTRODUCTION

Among Recent species of *Lymnaea* Lamarck, 1799 (*sensu* Hubendick, 1951), only the Hawaiian species *Lymnaea reticulata* (Gould, 1848) (Figures 1, 2) is distinguished by apparent consistent normal orthostrophic sinistrality (*sensu* Robertson, 1993). Among Recent normally dextral species, individual examples of sinistrality are rare. Baker (1911:1) acknowledged having seen only two specimens of normally dextral species with sinistral coiling of the shell. Populations of the widely distributed Old World *Lymnaea peregra* (Müller, 1774), an ambidextrous species (Robertson, 1993:112, 113), frequently include a small percentage (~3%) of sinistrally coiled individuals (Boycott et al., 1930). Recent work by Pierce (1993:985, 986) has presented evidence that ambidextrous sinistral coiling can also be found among fossil Lymnaeids. *Lymnaea ambiguspira* nom. nov. (formerly *L. vetusta ambigua* Pierce, 1993) from the Oligocene-Miocene of southwestern Montana, is one of two fossil ambidextrous species in which both sinistrally and dextrally coiled individuals are known to occur. The second species is *Lymnaea tulameenensis* (Russell, 1958), from the Oligocene of southern British Columbia. Search of the literature of North American paleontology failed to locate additional ambidextrous taxa. However, it appeared possible that consistent, or normally sinistral lymnaeid taxa, such as *L. reticulata*, might exist in the fossil record. Study and evaluation of these two ambidextrous species showed they are conchologically most similar to Recent *Lymnaea palustris* (Müller, 1774), which is known to very rarely produce a sinistrally coiled indi-

vidual (Baker, 1911:1), and should be considered related (ancestral?) to this Recent species. *Lymnaea reticulata* can also be considered closely related to *L. palustris*. Hubendick (1951:174) stated: "Disregarding this backward torsion the shell of *L. reticulata* is somewhat similar to the general shape of the shell of *L. palustris*."

MATERIALS AND METHODS

Paratypes of *Lymnaea ambigua* from the personal collection of Pierce, type specimens of *L. tulameenensis* and "*Aplexa ricei*" Russell, 1958, and of "*Physa*" *saxarubrensis* Russell, 1958, loaned by the Geological Survey of Canada (GSC), and Recent specimens of *L. reticulata* from Nuuanu, Island of Oahu, loaned by The Bishop Museum, were available for study. All measurements taken paralleled those used and defined by Hubendick (1951:fig. 2), with some change in nomenclature. Height, H, equates to 1 of Hubendick; Width, Wid., equates to b; and Height of aperture, Ha, equates to ml. Width of aperture was not measured. W/H and Ha/H are, respectively, ratios of the width to height of the shell, and height of the aperture to the overall height of the shell. Measurements of these parameters were made of large, apparently reproductively mature, specimens by ocular reticule with results in Table 1. Careful evaluation and measurements of these three species and comparison with the conchological characteristics of *L. palustris*, as defined by Hubendick (1951:119, 120), led to a set of criteria to be used in recognizing normally sinistral fossil Lymnaeids. These criteria are:



Explanation of Figures 1 to 12

Figures 1-8, $\times 5$; Figures 9-12, "natural size" (White, 1880). Figures 1-2. *Lymnaea reticulata* (Gould, 1848), Bishop Museum, BPBM, Lot 15014, Nuuanu, Oahu, Hawaii, 1. apertural view; 2. left lateral view. Figures 3-4. *Lymnaea ambiguspira* Pierce, nom. nov., 3. dextral holotype, Kansas University Museum of Invertebrate Paleontology (KUMIP) 236377, apertural view; 4. sinistral paratype, KUMIP 236378, apertural view. Figures 5-6 on one slab. *Lymnaea tulameenensis* Russell, 1958, 5. dextral paratype, Geological Survey of Canada (GSC) 11617, abapertural; 6. sinistral paratype, GSC 13283, apertural view (holotype of "*Aplexa ricei*"). Figures 7-8. *Lymnaea saxarubrensis* (Russell, 1958), 7. sinistral holotype GSC 13280, apertural view; 8. sinistral paratype GSC 13281, apertural. Figures 9-10. *Lymnaea disjuncta* (White, 1879), copies of plate 24, fig. 6a, b, of White (1880). 9. apertural view; 10. right lateral view. Figures 11-12. *Lymnaea bridgerensis* (Meek, 1873), copies of plate 19, fig. 10a, b, of White (1880), 11. apertural view; 12. abapertural view.

- (1) Whorls 5 or more, usually 6. (*L. reticulata* has 4 to 4.5).
- (2) Suture slightly impressed, whorls slightly rounded.
- (3) Apex usually acutely pointed.
- (4) Columella twisted, usually with plait or fold.
- (5) Ha/H usually < 0.50. (−0.60 or less for *L. reticulata*).

Based on these criteria, a review of the literature suggests that although there are examples of normally sinistral fossil lymnaeids, such are not common. These sinistral taxa range in age from Paleocene (questionably Cretaceous) to Miocene age and have been incorrectly assigned to either the genus *Physa* Draparnaud, 1801, or to the planorbid genus *Bulinus* Müller, 1781, which is not found in the Western Hemisphere. "*Bulinus*" *disjunctus* (White, 1879) is certainly a lymnaeid. "*Physa*" *saxarubrensis* (Russell, 1958) and "*P.*" *bridgerensis* (Meek, 1873) fit the criteria above and are almost certainly lymnaeids. Measurements, evaluation, and comparisons of "*B.*" *disjunctus* and "*P.*" *bridgerensis* were made using the excellent plates of White (1880: pl. 19, fig. 10, pl. 24, fig. 6; 1883: pl. 25, figs. 4, 5, pl. 30, figs. 9, 10).

SYSTEMATICS OF SINISTRAL LYMNAEIDAE

Family LYMNAEIDAE Rafinesque, 1815

Genus *Lymnaea* Lamarck, 1799

Type species: *Helix stagnalis* Linnaeus, 1758, by subsequent designation (Fleming, 1828).

Lymnaea palustris (Müller, 1774)

Description: Hubendick's (1951:119, 120) description of the shell of *Lymnaea palustris* follows: "The shell is ordinarily made up of six to seven gradually increasing whorls (fig. 302–303). The height of the aperture is between one third and one half of the total shell height. In *L. palustris* more than in any other Lymnaeid, the body whorl and even the whole shell has a tendency to become malleated. The apex is usually pointed but is sometimes obtuse. The suture is slightly impressed and the whorls slightly rounded. The aperture varies from roundly-ovate to long-ovate, usually not very expanded, and has very often a brownish or purplish line on the inner side of the peristome. A columellar fold generally occurs."

Remarks: The highly variable shell morphology for a given anatomical species of *Lymnaea*, resulting from the normal plasticity of the shell under varying environmental conditions, has led to a great number of named "species." Hubendick (1951) illustrated clearly the range of shell morphology for each species he recognized as valid based on anatomical criteria. Hubendick's *L. palustris*, through his synonymy, is approximated closely by the "group of *palustris*" of Baker (1911:298), and the *Stagnicola elodes* (Say, 1821) group of Burch (1989:176). From a paleontological standpoint, since only the shell is preserved, it is

most practicable to follow the classification of Hubendick. For further comments on this concept, see Pierce, 1993: 984–985.

Lymnaea ambiguspira Pierce, nom. nov.

(Figures 3, 4)

Lymnaea vetusta ambigua Pierce, 1993:985, 986, figs. 1.16–1.20, tables 4, 5.

Non *Lymnaea ambigua* Westerlund, 1881, Övers. Sv. Vet.-Ak. Förh. Stockholm 4:60

Non *Lymnaea ambigua* Pease, 1870, Amer. Jour. Conch. 6:6.

Lymnaea vetusta ambigua Pierce, 1993, is a primary homonym of *Lymnaea ambigua* Pease, 1870, and *L. ambigua* Westerlund, 1881, under the International Code of Zoological Nomenclature. The new name, *Lymnaea ambiguspira* is proposed as a replacement for the preoccupied *L. v. ambigua* Pierce, 1993; the type material remains the same.

Description: Shell of moderate size, usually dextral, occasionally sinistral, elongate conic; spire medium to high, acute, angle about 55°; width/height (W/H) about 0.50; whorls 6 to 6½, rounded to slightly flattened, suture shallowly impressed, near abutting; nuclear whorls about 1½, finely punctate, shining; subsequent whorls initially with weak, regular, slightly wavy, orthocline growth striae, becoming regularly costellate on last 1½ to 2 whorls, rarely malleated. Aperture D-shaped, modestly inflated, about one-half height of shell; outer lip thin, slightly curved, occasionally with internal varix shortly behind lip; inner lip broad, closely appressed, with distinct columellar plait. Umbilicus a narrow chink or closed (Pierce, 1993).

Remarks: Further study and comparison since initial publication of this taxon as a subspecies of *L. vetusta* Meek, 1860 has shown that, although *L. ambiguspira* and *L. vetusta* are closely related, *L. ambiguspira* differs sufficiently in shell morphology from the much older *L. vetusta* to preclude being considered conspecific. *Lymnaea ambiguspira* tends to be shorter, 7–10 mm in mature specimens compared to about 14 mm for *Lymnaea vetusta*, with more whorls (6–6.5), less acute apex, 55° compared to 45°, and greater W/H, 0.50 compared to 0.46. *Lymnaea ambiguspira* is regular costellate on last 1.5 to 2 whorls, occasionally becoming malleated on very large specimens. Its aperture is more inflated with a less angular basal margin, and a curving columellar plait when compared to *L. vetusta*. The tendency to ambidexterity observed in *L. ambigua* is highly variable. Sinistral individuals represented less than 1% at one locality and 55% at the second locality (Pierce, 1993:985, 986, tables 4, 5).

Material: More than 600 specimens were found at eight localities in southwestern Montana, ranging in age from middle Oligocene (Whitneyan?) through early Miocene (late Arikarean). Sinistral individuals were restricted to only two of the localities, both late Oligocene (early Arikarean).

Table 1

Measurements (in mm) of sinistral Lymnaeidae. E = estimated from measurements of White's (1880, 1883) plates; Max. = largest specimen available; ¹ = LaRocque, 1960, p. 40; ² = Meek, 1870, p. 517.

		Ht.	Wid.	W/H	Wh.	Ha	Ha/H
<i>Lymnaea reticulata</i> (n = 6) (Recent BPBM Lot #'s 15014 & 17365)							
Sinistral only	Max.	9.0	5.2	0.58	4.25	5.4	0.60
	Min.	6.0	3.6	0.60	3.33	3.7	0.62
	Ave.	7.68	4.50	0.59	3.97	4.58	0.60
<i>Lymnaea ambiguspira</i> (late Oligocene to early Miocene)							
Dextral	Max.	10.2	5.0	0.49	6.2	5.2	0.51
Sinistral	Max.	10.3	5.15	0.50	6.25	4.85	0.47
<i>Lymnaea tulameenensis</i> (middle to late Oligocene)							
Dextral	Max.	12.0	4.4	0.37	8.25	4.0	0.33
Sinistral	Max.	13.6	5.4	0.40	7.0	5.3	0.39
<i>Lymnaea saxarubrensis</i> (middle to late Oligocene)							
Sinistral only	Max.	11.4	5.4	0.47	5.5	6.3	0.55
<i>Lymnaea disjuncta</i> (?Cretaceous to early Eocene)							
Sinistral only		E44.0	E20.0	0.45	6	E21.0	0.48
<i>Lymnaea bridgerensis</i> (Paleocene, Oligocene)							
Sinistral only		E39.0 (29.2) ²	E21.0 (16.8) ²	0.54 (0.57) ²	5-6 ¹	E21.0	0.54

Lymnaea tulameenensis Russell, 1958

(Figures 5, 6)

Stagnicola tulameenensis Russell, 1958:88, pl. I, figs. 2-4.

Aplexa ricei Russell, 1958:90, pl. II, fig. 6.

Description: Russell's (1958:88) original description of the holotype, GSC 11616, follows: "Shell small, slender, volutions about six. Spire slender, whorls gently convex, apex rounded. Aperture about two-fifths total length of shell, narrowly ovoid, inner lip thickened. Surface with fine growth lines. Length of type, 6.9 mm; width, 2.9 mm; length of aperture, 2.5 mm." (Russell 1958:88). Emendation: inner margin of basal lip of aperture reflected slightly; columella twisted and with columellar fold at about mid-height; apex roundly pointed; with faint col-labral costae on last three whorls. Ambidextrous; both sinistral and dextral morphs occur. Height of paratype, GSC 11617, 12.0 mm; width 4.4 mm; height of aperture 4.0 mm; W/H 0.37; Ha/H 0.33; whorls 8.25.

Remarks: *Lymnaea tulameenensis* was recognized as a species with both dextral and sinistral morphs when *L. ambiguspira* was first being studied. Russell selected a small, perhaps not reproductively mature, individual of only 6.25 whorls for his holotype, GSC 11616. He only provisionally referred a larger individual, GSC 11617, to the species. Examination of both holotype and paratype resulted in emendations to the description above. Russell's (1958:90) description of "*Aplexa ricei*," the sinistral morph of *L. tulameenensis*, is as follows: "Shell rather small, delicate,

slender; spire long and tapering; volutions five, gently convex. Aperture narrowly ovoid; distinctly less than half length of shell; inner lip thin, but with distinct columellar fold about mid-length. Surface with very faint but regular growth lines. Length of type, 13.2 mm; width, 5.4 mm; length of aperture 5.6 mm." Examination of the holotype, GSC 13283, disclosed several differences from the description above. The most significant are that the whorls are about seven rather than five as reported, and the description fails to mention that the inner margin of the basal lip is reflected, the columella is twisted, and weak col-labral costellae are present on the last two to three whorls. When both amplified descriptions are compared, it becomes apparent that "*Aplexa ricei*" is an orthostrophic sinistral morph of *Lymnaea tulameenensis*. Viewing the two specimens, the paratype of *L. tulameenensis* and the holotype of "*A. ricei*," lying almost apex to apex on the same rock slab, leaves no doubt. Russell (1958:86) was somewhat ambiguous as to the age of the Princeton fauna. Although the associated flora, insects, and fish are typical of the middle Oligocene to Miocene, he stated that at least part of the unit had to be of middle Eocene age based upon two mammal teeth found nearby. Such teeth, at least in younger sediments, may be reworked. Based on the preponderance of evidence, this fauna is considered middle to late Oligocene herein.

Material: Unfortunately, the number of individuals available for study is quite small, only two dextral specimens (GSC 11616, holotype and GSC 11617, paratype) and one sinistral specimen (GSC 13283, holotype of "*A. ricei*").

Lymnaea saxarubrensis (Russell, 1958)
(Figures 7, 8)

Physa saxarubrensis Russell, 1958:89–90, pl.II, figs. 1–4.

Description: Russell's (1958:89) original description follows: "Shell small, robust, moderately elongated; volutions five, convex; spire rather long, apex rounded. Aperture ovoid, not expanded, length a little more than half that of shell; inner lip with slight columellar fold. Surface marked by well-defined growth lines and on some specimens by a resting varix on the body whorl. Length of type, 9.7 mm; width, 4.9 mm; length of aperture, 5.2 mm." Emendation: columella twisted; apex roundly pointed; with collabral costae on last whorl, about 3 per millimeter. Measurements of holotype, GSC 13280: height 11.4 mm; width 5.4 mm; apertural height 6.3 mm; whorls 5.5. Measurements of paratype, GSC 13281: height 9.9 mm; width 5.0 mm; apertural height 4.7 mm; whorls 5, estimated.

Remarks: Since all type specimens from the Russell's (1958) Princeton fauna, southern British Columbia, were at hand, direct measurements of the holotype and paratype of *L. saxarubrensis* could be made. The discrepancy in measurements of the holotype is not understood. Russell (1958: 89–90) commented that "the present species is in contrast to most of those in the Recent fauna in having a spire almost as long as the aperture, and in lacking any inflation of the body whorl," and compared "*P.*" *saxarubrensis* to "Cretaceous and early Tertiary species such as *P. canadensis* Whiteaves, '*P.*' *disjunctus* (White), and '*P.*' *bridgerensis* Meek." The first, *P. canadensis*, does appear to be a physid. The last two are shown to be sinistrally coiled lymnaeids herein.

Material. Only two specimens were available, the holotype, GSC 13280, and a paratype, GSC 13281. Age is considered to be middle to late Oligocene.

Lymnaea disjuncta (White, 1879)
(Figures 9, 10)

Bulinus disjunctus White, 1879:165, 170, 241, 255; 1880:55, 86, pl. 24, fig. 6; 1883:451, pl. 25, figs. 4, 5.
Aplexa disjuncta (White), Henderson, 1935:263.

Description: White's (1880:86, 87) original description follows: "Shell rather large and moderately elongated; volutions about six, those of the spire increasing gradually in size, but the body volution is proportionally more inflated than those of the spire; suture distinct, but not very deep, and not conspicuous, because of the moderate convexity of the volutions; length of the spire a little more than half that of the whole shell; callus of the inner lip broad, its posterior half closely appressed against and adherent to the body; its anterior half deflected or disjoined from the body, so as to leave a kind of umbilical space between it and the body of the shell. This condition of the inner lip is evidently not accidental, as it is present on all

the examples, young and old, that have yet been found; aperture moderately large, its length a little more than half the full length of the shell. Surface marked only by the fine lines of growth peculiar to the Physidae.

"Length, about 43 millimeters; breadth of body volution, 20 millimeters."

Remarks: The last sentence in the description, before the measurements, is misleading. Fine lines of growth are not peculiar to the Physidae. No mention of spiral sculpture, found on so many physids, is found. White's description is confused as to the relative length of the spire and of the aperture. Measurements from his plates result in an Ha/H of 0.48. The age of this species is not clear; it could range from very latest Cretaceous to early Eocene. Comparisons were made using published descriptions and illustrations.

Lymnaea bridgerensis (Meek, 1873)
(Figures 11, 12)

Physa bridgerensis Meek, 1873:516; White, 1880:45, pl. 19, fig. 10; 1883:450, pl. 30, figs. 9, 10; Henderson, 1935: 258; LaRocque, 1960:40, pl. 3, fig. 27, *non* figs. 28, 29.

Description: Meek's (1873:516) original description follows: "Shell attaining a large size, subovate in form; spire prominent, conical; volutions four and a half to five, moderately convex, last one large but not very ventricose; suture well defined; aperture narrow-subovate, arcuate, acutely angular above, about twice as long as the spire; columella twisted into a rather prominent fold. Surface with fine, sharp lines of growth.

"Length about 1.15 inches; breadth, 0.66 inch."

Remarks: LaRocque (1960:40, pl. 3, fig. 27) illustrated and described this species from the Paleocene Flagstaff Formation of Utah. His figure 27 is certainly *L. bridgerensis*; however, his figures 28 and 29, also identified as this species, are of a short-spined, inflated physid. His measurements correspond closely with those given in the type description, and taken from White's plate (1880:pl. 19, fig. 10), except that LaRocque counted six whorls on his illustrated hypotype, Ohio State University 20064. Age of the type locality is middle to upper Eocene.

CONCLUSIONS

The search for fossil sinistral lymnaeids in North America disclosed two ambidextrous species, *L. ambiguuspira* and *L. tulameenensis*, in which both orthostrophic sinistral and dextral morphs are found in the same population. These taxa are of middle Oligocene to early Miocene age. Three species, *L. saxarubrensis*, *L. disjuncta*, and *L. bridgerensis*, were found that exhibit apparent normal orthostrophic sinistrality. These taxa range in age from early Eocene (questionably late Cretaceous) to late Oligocene. It appears that sinistral coiling among the Lymnaeidae has always been a rare occurrence, being most common in the middle to late Oligocene when three species displayed

this tendency. It is tempting to speculate that the Recent Hawaiian *Lymnaea reticulata* is the result of adventitious avian dispersal of one of these mid-Tertiary species to a newly emergent and isolated island environment.

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